

Biodiversity of *Spongosorites coralliophaga* (Stephens, 1915) on coral rubble at two contrasting cold-water coral reef settings

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Abstract Cold-water coral reefs (CWRs) in the northeast Atlantic harbor diverse sponge communities. Knowledge of deep-sea sponge ecology is limited and this leaves us with a fragmented understanding of the ecological roles that sponges play in CWR ecosystems. We present the first study of faunal biodiversity associated with the massive demosponge *Spongosorites coralliophaga* (Stephens, 1915) that typically colonizes coral debris fields of CWRs. Our study focused on the sessile fauna inhabiting sponges mixed with coral rubble at two contrasting settings in the northeast Atlantic: the shallow inshore (120–190 m water depth) Mingulay Reef Complex (MRC) and the deep offshore (500–1200 m) Logachev Mound (LM) coral province. MRC is dominated by the scleractinian *Lophelia pertusa*, while LM is dominated by *L. pertusa* and *Madrepora oculata*. Nine sponge–coral rubble associations were collected from MRC and four from LM. Measurements of abundance, species richness, diversity, evenness, dry biomass, and composition of sessile fauna on sponge and coral rubble microhabitats were undertaken. Differences in community composition between the two

regions were mainly a response to changes in fauna with depth. Fauna composition was also different between sponge and coral rubble within each region. Infauna constituted a minor component of the sponge-associated fauna in MRC but had a higher contribution in LM. Sponge and coral rubble sessile fauna in both regions was mainly composed of cnidarians and molluscs, similarly to some previous studies. Sponges' outer surfaces at MRC were colonized by a species-rich community with high abundance and biomass suggesting that *S. coralliophaga* at MRC acts as a settlement surface for various organisms but such a role is not the case at LM. This difference in the role of *S. coralliophaga* as a biological structure is probably related to differences in fauna composition with depth, bottom current speed, and the quantity/quality of food supplied to the benthos.

Keywords Porifera · Symbionts · Microhabitats · Biodiversity

Introduction

Sponges (Phylum Porifera) constitute a highly diverse faunal group that create ecologically significant biological structures (Buhl-Mortensen et al. 2010; Hogg et al. 2010) as they supply substrate for attachment, food particles, and shelter from predation to various epifaunal organisms (Bell 2008 and references therein; Wulff 2012 and references therein). Recent evidence has shown that shallow-water sponges may play a key role in reef food webs through their ability to convert dissolved to particulate organic matter which is subsequently made available to reef fauna, thus enabling hot spots of diversity and biomass to persist in oligotrophic environments (de Goeij et al. 2013). In addition, sponges harbor diverse microbial communities

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which are involved in a number of nitrogen-processing pathways such as nitrification, nitrogen fixation, denitrification, and anammox (Fiore et al. 2010 and references therein; Ribes et al. 2012; Han et al. 2013); however, due to the complexity of these processes (e.g., Hoffmann et al. 2009), our knowledge of the role of sponges in nitrogen cycling at local, regional, or global scale remains very limited (Maldonado et al. 2012).

In comparison with shallow-water ecosystems, knowledge of the physiology and ecology of deep-sea sponges is still very limited (Witte and Graf 1996; Witte et al. 1997; Pile and Young 2006; Yahel et al. 2007), as is knowledge of their role as biological structures (Klitgaard 1995; Beaulieu 2001; Buhl-Mortensen et al. 2010). This hampers our understanding of the deep-sea ecosystem functions provided by sponge habitats. In the cold-water coral reefs (CWRs) of the northeast Atlantic Ocean, recent studies have described a diverse community of associated sponges (van Soest and Lavaleye 2005; van Soest et al. 2007; Roberts et al. 2009). CWRs are themselves ecosystems with high ecological and economic values, and they are very sensitive to anthropogenic disturbance (Roberts et al. 2009; Henry et al. 2013b); thus, knowledge of their structure and function is a prerequisite for the implementation of efficient management strategies (Henry et al. 2013a).

The present study investigates the fauna living in association with the demosponge *S. coralliophaga* (Stephens, 1915) and its underlying coral rubble at two CWRs of the northeast Atlantic, aiming to provide a first insight into the contribution of this species to the structure of the reef and especially to habitat complexity and biodiversity. *S. coralliophaga* is abundant in CWRs and is characterized by its massive body form and extensive colonization of coral rubble (van Soest et al. 2007; Vad 2013).

Materials and methods

Collection of samples

Specimens of the sponge *S. coralliophaga* that had colonized coral rubble and the associated fauna were collected by the remotely operated vehicle (ROV) *Holland I* in two contrasting settings, Mingulay Reef Complex (MRC) and Logachev Mounds (LM), in May/June 2012 during the Changing Oceans 2012 expedition on board the Royal Research Ship (RRS) *James Cook* (JC073 cruise; Roberts and shipboard party 2013; Table 1; Fig. 1). *S. coralliophaga*, being large in size and yellow in color (Fig. 2), was easily identified during ROV surveys. After its collection from the seafloor using the ROV manipulator arm, the sponge–coral rubble association was carefully transferred

Table 1 Locations of sample collection at Mingulay Reef Complex (MRC) and Logachev Mound (LM)

Location	Depth (m)	Latitude	Longitude
MRC	127	56°49.3'N	7°23.6'W
	128	56°49.3'N	7°23.6'W
	127	56°49.3'N	7°23.6'W
	131	56°49.3'N	7°23.7'W
	122	56°49.3'N	7°23.6'W
	128	56°49.3'N	7°23.6'W
	128	56°49.3'N	7°23.6'W
	131	56°49.3'N	7°23.6'W
	131	56°49.3'N	7°23.6'W
	131	56°49.3'N	7°23.6'W
LM	800	55°29.6'N	15°49.2'W
	683	55°29.6'N	15°49.1'W
	683	55°29.6'N	15°49.1'W
	683	55°29.6'N	15°49.1'W

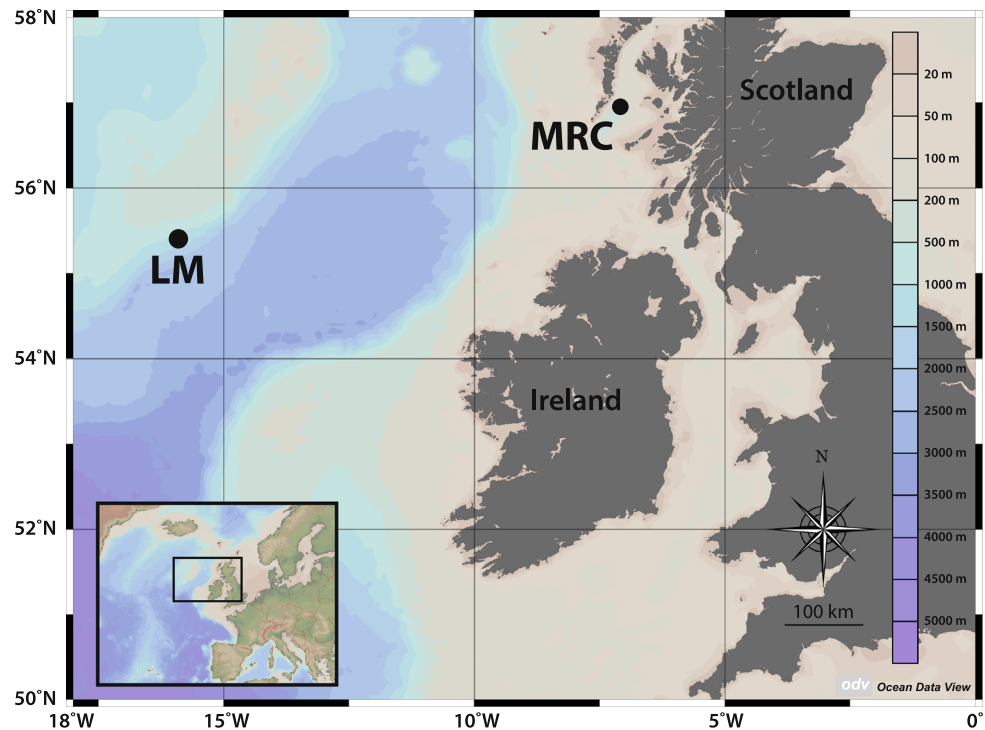
to the ROV biobox, a storage compartment that closes once withdrawn beneath the vehicle and during recovery to the surface.

The MRC in the Outer Hebrides Sea comprises live coral reef areas at 120–190 m depth, dominated by the scleractinian *Lophelia pertusa* (Roberts et al. 2005, 2009). Hydrographic surveys have revealed a south-southwest (SSW) to north-northeast (NNE) direction in major surface and seabed flows, as well as the importance of rapid downwelling of surface water and advection of deep bottom water as mechanisms of food supply for the reef communities (Davies et al. 2009; Roberts et al. 2009; Duineveld et al. 2012; Findlay et al. 2014; Moreno Navas et al. 2014). In the MRC area, hydrographic and bathymetric variables have been predicted to be responsible for community variation across broader spatial scales while recruitment, intra- and interspecific social interactions, and food supply seem to play a greater role in the fine-scale assembly of communities (Henry et al. 2010, 2013a).

In contrast to the shallow inshore setting of the MRC, the LM are large offshore carbonate mounds situated on the southeast Rockall Bank (500–1200 m depth; van Weering et al. 2003) dominated by *L. pertusa* and *Madrepora oculata* (van Weering et al. 2003; Duineveld et al. 2007). Hydrographic studies in the area have demonstrated the importance of advection in sustaining the food supply to the LM reef community (Duineveld et al. 2007), with recent modeling studies highlighting the importance of coral carbonate mound structure in promoting local vertical mixing and organic matter flux to the benthos (Mohn et al. 2014).

Nine *S. coralliophaga*–coral rubble samples were collected at MRC and four at LM (Table 1; Fig. 2a–e).

Fig. 1 Sites of sample collection. Mingulay Reef Complex (MRC) and Logachev Mound (LM)



Immediately after collection by the ROV, these samples were fixed in 10 % seawater formalin.

Sample processing

In the laboratory, the sponge–coral rubble associations were initially examined for the presence of fauna: (1) on outer sponge surface; (2) on coral rubble; and (3) on secondary biogenic structures (i.e., species living on the outer sponge surface/coral rubble and which were later colonized by other epifaunal organisms). Thereafter, sponges were carefully dissected with a scalpel and the internal structures (i.e., canals, cavities) were examined for the presence of infaunal organisms. All specimens collected were identified to the lowest possible taxonomic level with help from specialists, and the number of individuals from each association was recorded. Furthermore, the individuals from each association were dried at 60 °C for 48 h before their dry weight was recorded (± 0.01 mg). In addition, the volume of dried sponge (60 °C, 48 h) and the volume of coral rubble were measured through the water displacement method (± 1 cm³; Ribeiro et al. 2003; Fiore and Jutte 2010).

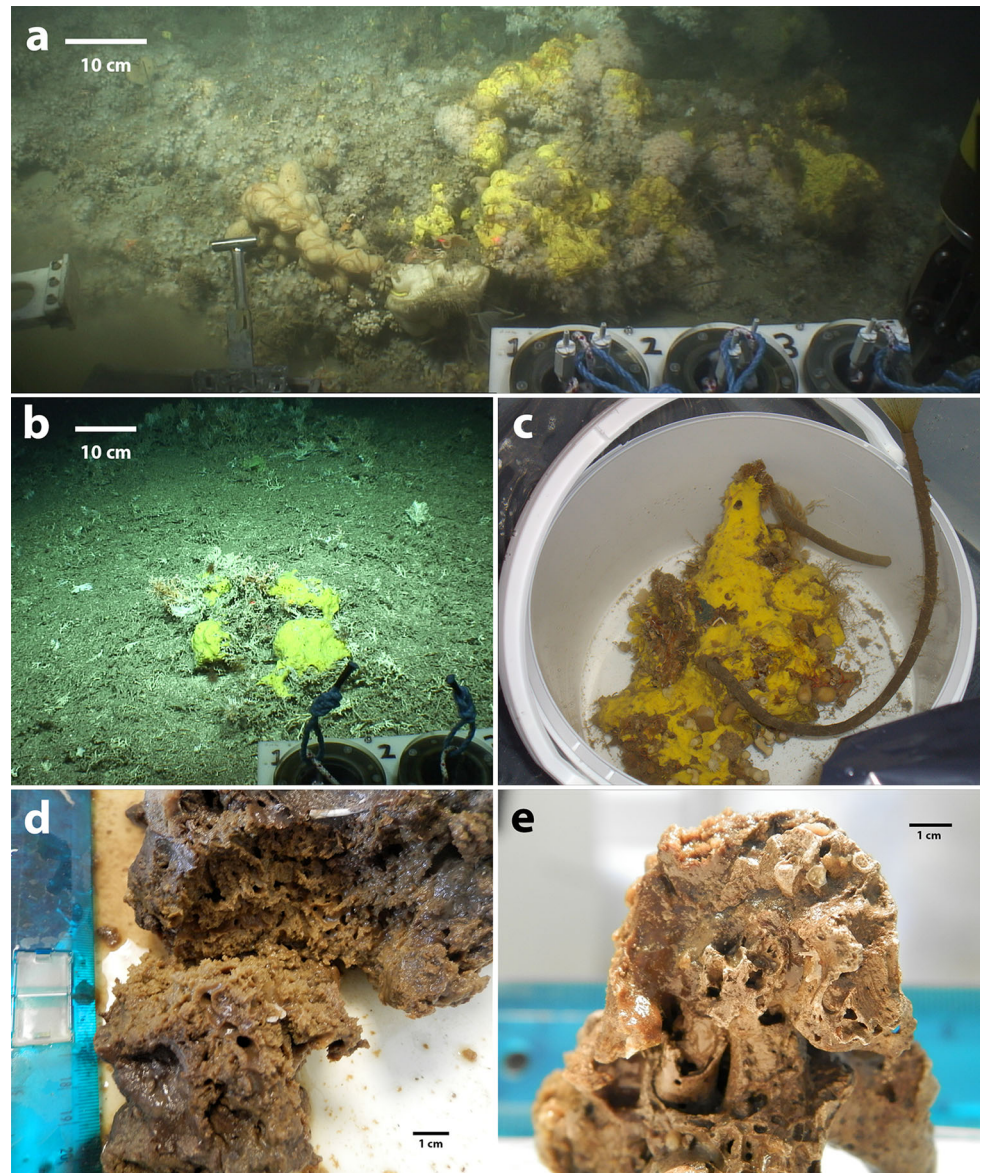
Only living specimens were taken into account in the numerical/statistical analyses described below. Each species of the sessile fauna was assigned to one (or both) of the two microhabitats—*S. coralliophaga* and/or coral rubble. Sponge infauna was assigned to the *S. coralliophaga* microhabitat. The individuals that were found on secondary

biological structures were incorporated accordingly (e.g., foraminiferans that had colonized hydroids living on outer sponge surface were grouped into the *S. coralliophaga* microhabitat). Specimens of mobile fauna (see Table 2 for details) were not assigned to microhabitats and thus were not taken into account in the comparisons between sponge and coral rubble. Allocation of the sessile fauna and sponge infauna to microhabitats was used to group samples a priori as follows: (1) MRC sponge, (2) MRC coral rubble, (3) LM sponge, and (4) LM coral rubble. In addition to a microhabitat, each species of the sessile fauna and sponge infauna was attributed a feeding guild (suspension/filter feeder, predator, deposit feeder/grazer); this characterization was based mainly on information available in Henry et al. (2013a). For a number of species, information on the feeding type was collected from Vader (1983) (amphipods), Neves and Omena (2003) (polychaetes), Nielsen and Riisgard (1998), Bader and Schafer (2005) (bryozoans). For two species the characterization of their feeding type was not possible due to the absence of sufficient taxonomic resolution.

Data analysis

The software PRIMER6 (Primer-E Ltd; Clarke and Warwick 2001) was used for the analyses of community structure. Data on the number of individuals and dry biomass, both normalized to volume of microhabitat, were fourth-root transformed and were used in the calculation of

Fig. 2 **a** *Spongosorites coralliophaga* at Mingulay Reef Complex (MRC), **b** *S. coralliophaga* at Logachev Mound (LM), **c** Outer surface of *S. coralliophaga* colonized by a diverse faunal community, **d** internal canals and cavities, **e** underlying coral rubble colonized by *S. coralliophaga*



Bray–Curtis similarities and similarity matrices. Based on these matrices, non-metric multi-dimensional scaling (nMDS) 2-dimensional (2D) plots were constructed incorporating the four groups of samples mentioned above. In the constructed 2D plots, the values of stress were lower than 0.2 indicating a good ordination (Clarke 1993; Clarke and Warwick 2001). One-way analysis of similarities (ANOSIM) was carried out to check for significant differences between groups (i.e., MRC sponge vs. MRC coral rubble, MRC sponge vs. LM sponge, MRC coral rubble vs. LM coral rubble, and LM sponge vs. LM coral rubble), using data of individuals cm^{-3} microhabitat and dry biomass cm^{-3} microhabitat. These data were also used to identify the species that were responsible for the average

dissimilarity between groups (SIMPER analysis). From the analyses mentioned above, we had to exclude two outlier samples—one sponge sample from LM and one coral rubble sample from MRC—which skewed the presentation of the nMDS 2D plots.

PRIMER6 was also used to calculate two biodiversity indices, Shannon–Wiener H' (estimated using Log e) and Pielou's evenness J' (Pielou 1975). For these two biodiversity indices, and for the number of species $S \text{ cm}^{-3}$ microhabitat, the number of individuals cm^{-3} microhabitat, and the dry biomass cm^{-3} microhabitat, the normality of the distributions was checked with the Shapiro–Wilk test. In the case of normal distributions and equal variances, the existence of significant differences between groups was

Table 2 Taxonomic groups living in association with *Spongosorites coralliophaga* and its underlying coral rubble in the cold-water coral reefs (CWRs) of the Mingulay Reef Complex (MRC) and Logachev Mound (LM) in the northeast Atlantic Ocean

Taxonomic group	Locations and microhabitats					
	MRC sponge outer surface	MRC sponge inner surface	MRC coral rubble	LM sponge outer surface	LM sponge inner surface	LM coral rubble
Foraminifera						
Morphotype 1 foraminifera	+ ^a	+ ^b	+ ^c			+/ ^d
Morphotype 2 foraminifera		+				
Morphotype 3 foraminifera		+ ^{e*}				
Porifera						
<i>Haliclona (Haliclona) urceolus</i> (Rathke and Vahl, 1806)	+					
<i>Poecillastra compressa</i> (Bowerbank, 1866)	+					
Porifera sp.	+					
Hydrozoa						
<i>Acryptolaria conferta</i> (Allman, 1877)						+
<i>Clytia hemisphaerica</i> (Linnaeus, 1767)	+ ^f					
<i>Halecium labrosum</i> Alder, 1859			+			
<i>Halecium muricatum</i> (Ellis and Solander, 1786)			+			
<i>Halecium</i> sp.	+	+ [*]				
Hydrozoa sp.				+		
<i>Kirchenpaueria</i> sp.	+					
<i>Modeeria rotunda</i> (Quoy and Gaimard, 1827)	+ ^{a,b}					
<i>Rosalinda williamsi</i> Totton, 1949	+/ ^g					
<i>Zanclaea sessilis</i> (Gosse, 1853)	+					
<i>Zygophylax pinnata</i> (Sars, 1873)						+
Anthozoa						
Anthozoa sp.	+					
<i>Corynactis viridis</i> Allman, 1846				+		
<i>Edwardsiella carnea</i> (Gosse, 1856)		+				
cf <i>Edwardsiella loveni</i>						+
<i>Paraedwardsia sarsii</i> (Dueben and Koren, 1847)				+		
<i>Parazoanthus anguicomus</i> (Norman, 1868)	+/ ^h	+ [*]	+	+		+
<i>Telestula</i> sp.						+
Nematoda						
Nematoda sp.			?			
Polychaeta						
cf Aphroditidae						?
<i>Bispira volutacornis</i> (Montagu, 1804)	+					
<i>Branchiommia bombyx</i> (Dalyell, 1853)			?			
<i>Capitella</i> sp.						?
<i>Eunice dubitata</i> Fauchald, 1974			?			?
<i>Eunice pennata</i> (Müller, 1776)			?			
<i>Euphrosine</i> cf <i>borealis</i>			?			?
cf <i>Fimbriosthenelais zetlandica</i>			?			
<i>Haplosyllis spongicola</i> (Grube, 1855)		+				?
cf <i>Leocrates atlanticus</i>						?
<i>Lepidonotus</i> sp.			?			
<i>Lumbrineris tetraura</i> (Schmarda, 1861)						?
<i>Myrianida</i> sp. 1			?			

Table 2 continued

Taxonomic group	Locations and microhabitats					
	MRC sponge outer surface	MRC sponge inner surface	MRC coral rubble	LM sponge outer surface	LM sponge inner surface	LM coral rubble
<i>Myrianida</i> sp. 2						?
<i>Nereimyra punctata</i> (Müller, 1788)			?			
cf <i>Notophyllum foliosum</i>						?
cf Sabellidae			?			
Scalibregmatidae sp.						?
<i>Serpula vermicularis</i> Linnaeus, 1767		+				
Sigalionidae sp.			?			?
Syllidae sp.			?			?
Terebellidae sp.			?			
<i>Trypanosyllis zebra</i> (Grube, 1860)			?			?
Entoprocta						
<i>Pedicellina hispida</i> Ryland, 1965		+				
Crustacea						
Amphipoda sp. 1			?			
Amphipoda sp. 2			?			
Amphipoda sp. 3			?			
Amphipoda sp. 4						?
<i>Aristias neglectus</i> Hansen, 1888		+				
<i>Galathea strigosa</i> (Linnaeus, 1761)			?			
<i>Janira maculosa</i> Leach, 1814		+			+	
cf <i>Laetmatophilus tuberculatus</i>						?
<i>Munna</i> sp.			?			
<i>Scalpellum scalpellum</i> (Linnaeus, 1767)	+ ⁱ					
Mollusca						
<i>Asperarca nodulosa</i> (O. F. Müller, 1776)						+
<i>Berthella</i> sp.						?
<i>Delectopecten vitreus</i> (Gmelin, 1791)						+
cf <i>Diodora graeca</i>						?
<i>Emarginula fissura</i> (Linnaeus, 1758)			??*			
<i>Hiatella arctica</i> (Linnaeus, 1767)		+/+*	+			
<i>Modiolula phaseolina</i> (Philippi, 1844)		+	+			
<i>Heteranomia squamula</i> (Linnaeus, 1758)	+ ^j	+*	+/+ ^c			
<i>Lima marioni</i> Fischer, 1882						+
Nudibranchia sp.	?					
<i>Palliolum striatum</i> (O. F. Müller, 1776)			+			
<i>Pseudamussium sulcatum</i> (Müller O. F., 1776)						+
<i>Puncturella noachina</i> (Linnaeus, 1771)						?
Solenogastres sp.						?
cf <i>Tonicella marmorea</i>				?		
Bryozoa						
<i>Chartella barleei</i> (Busk, 1860)	+/+ ^k	+*				
Candidae sp.	+					
<i>Disporella hispida</i> (Fleming, 1828)		+				
<i>Idmidronea atlantica</i> (Forbes, in Johnston, 1847)			+			
<i>Reteporella beaniana</i> (King, 1846)			+		+	+

Table 2 continued

Taxonomic group	Locations and microhabitats					
	MRC sponge outer surface	MRC sponge inner surface	MRC coral rubble	LM sponge outer surface	LM sponge inner surface	LM coral rubble
<i>Schizomavella linearis</i> (Hassall, 1841)		+				
Brachiopoda						
<i>Terebratulina retusa</i> (Linnaeus, 1758)			+			
<i>T. septentrionalis</i> (Couthouy, 1838)						+
Brachiopoda sp.		+*				
Echinodermata						
<i>Cidaris cidaris</i> (Linnaeus, 1758)						?
cf Goniasteridae sp.						?
Holothuroidea sp.						?
<i>Ophiothrix fragilis</i> (Abildgaard, in O.F. Müller, 1789)	?					
<i>Ophiura ophiura</i> (Linnaeus, 1758)	?			?		
Ophiuroidea sp.	?					
<i>Ophioctenella acies</i> Tyler et al. 1995				?		
<i>Porania (Porania) pulvillus</i> (O.F. Müller, 1776)			?			
Ascidiacea						
<i>Ascidia mentula</i> Müller, 1776						+
<i>Polycarpa pomaria</i> (Savigny, 1816)	+	+*				

Allocation of microhabitat has only been carried out for sessile fauna and sponge infauna. Footnotes denote secondary biogenic structures; ?, microhabitat not known with precision; *, specimen's remnants/no tissue presence/shell overgrown by *S. coralliophaga*

^a *Halecium* sp.

^b Unidentified hydrozoan stems

^c *Halecium muricatum*

^d *Zygophylax pinnata*

^e Recorded in microscopic sections of *Poecillastra compressa* inner surface

^f *Modeeria rotunda*

^g Tubeworm casings

^h *Poecillastra compressa*

ⁱ *Bispira volutacornis*

^j *Rosalinda williamsi*

^k *Polycarpa pomaria*

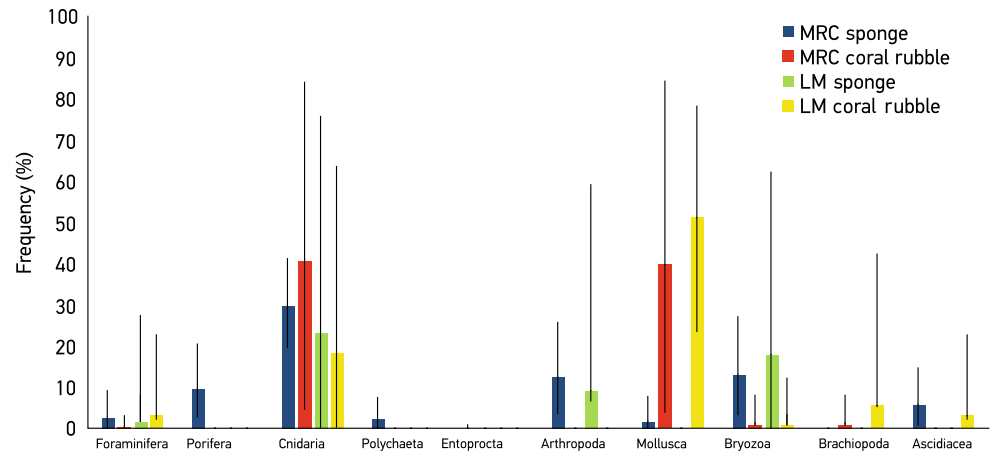
tested with a two-sample *t* test. In the case of normal distributions with unequal variances, a Welch's two-sample *t* test was used. When the distribution was not normal, a Wilcoxon rank sum test was carried out or a square-root transformation was performed where appropriate. Correlations between microhabitat volume and *S*, *H'*, *J'*, total number of individuals and total dry biomass were calculated using Pearson's product-moment correlation coefficient or Spearman's rank correlation coefficient. Square-root transformation was used where appropriate. Examination of (a) differences between groups and (b) correlations were carried out in the statistical analysis environment R (R Core Team 2013).

Results

Community composition and structure

In total, 91 species of sessile and mobile fauna belonging to 12 phyla were recorded (Table 2) and comprised 2525 individuals. The highest species numbers were attributed to Annelida (25.3 %), Cnidaria (19.8 %), and Mollusca (16.5 %). The relative presence of the taxonomic groups of the sessile fauna and sponge infauna in each of the microhabitats can be seen in Fig. 3. A total of 34.1 % of the species were recorded solely at LM, 53.8 % solely at MRC, and only 12.1 % were common between the two

Fig. 3 Relative contribution (%) of taxonomic groups of the sessile fauna and sponge infauna to each of the microhabitats in Mingulay Reef Complex (MRC) and Logachev Mound (LM). Calculations based on back-transformed data of arcsine numbers. Bars denote the mean values. Error bars show upper and lower 95 % CI



regions. The common species included the anthozoan *Parazoanthus anguicomus* (Norman, 1868), the polychaetes *Eunice dubitata* (Fauchald, 1974), *Haplosyllis spongicola* (Grube, 1855), *Trypanosyllis zebra* (Grube, 1860), *Euphrosine cf borealis*, Sigalionidae sp., Syllidae sp., the isopod *Janira maculosa* (Leach, 1814), the bryozoan *Reteporella beaniana* (King, 1846), the ophiuroid *Ophiura ophiura* (Linnaeus, 1758) and “Morphotype 1 foraminifera”. Out of the 60 species recorded at MRC, eight were recorded for first time on this CWR including the hydrozoans *Halecium labrosum* (Alder, 1859) and *Kirchenpaueria* sp., the polychaetes *Myrianida* sp.1, *Bispira volutacornis* (Montagu, 1804), *Eunice dubitata*, *Eunice pennata* (Müller, 1776), and *Haplosyllis spongicola*, and the cirripedian *Scalpellum scalpellum* (Linnaeus, 1767). Also, to the best of our knowledge, this is the first record of the ophiuroid *Ophioctenella acies* Tyler et al. 1995 in a non-chemosynthetic ecosystem (Stöhr and Segonzac 2005).

In both regions only a small number of species (12 in MRC and 2 in LM) were found inside the sponge (Table 2). Infauna constituted a minor component, both in terms of abundance (total number of individuals) and dry biomass (total mg), of the total sponge-associated fauna in MRC, but had a higher contribution in LM (Fig. 4). In regard to the infauna, species with the highest number of individuals in total included the amphipod *Aristias neglectus* (62 specimens), and the species with the highest biomass was the bryozoan *Reteporella beaniana* (156.8 mg).

At MRC, a number of epifaunal species were found on secondary biological structures, for example “Morphotype 1 foraminifera” were exclusively recorded on the stems of the hydroids *Halecium* sp. and *H. muricatum* (Ellis and Solander, 1786), and *S. scalpellum* was found exclusively attached to the tube of *B. volutacornis*. At LM, the only secondary biological structure was the hydroid *Zygophylax*

pinnata (Sars, 1873), which hosted a small number of “Morphotype 1 foraminifera”. Furthermore, at MRC, a number of species were present at more than one microhabitat, e.g., *Hiatella arctica* was recorded both inside sponge as well as on coral rubble, while *Heteranomia squamula* was recorded on coral rubble as well as on the stems of the hydroid *Rosalinda williamsi* Totton, 1949 (Table 2). At LM associations, only “Morphotype 1 foraminifera” were recorded both on hydroid stems and coral rubble.

The nMDS 2D-ordination plots based on number of individuals cm^{-3} microhabitat and dry biomass cm^{-3} microhabitat for sessile fauna and sponge infauna revealed a trend for distinct groups both in terms of location/depth and microhabitat (Fig. 5). These trends were also confirmed by one-way ANOSIM analysis using individuals cm^{-3} microhabitat and dry biomass cm^{-3} microhabitat (Table 3). All the groups that were compared showed significant differences; the highest values recorded were between MRC sponge and LM sponge and the lowest values were between MRC coral rubble and LM coral rubble. The discrimination between LM sponge and LM coral rubble samples was higher than between MRC sponge and MRC coral rubble samples. The high *R* values confirmed the limited overlap between different microhabitats within the same location, as well as in the same type of microhabitat between the two different locations.

In terms of the number of individuals cm^{-3} microhabitat, SIMPER analysis revealed an average dissimilarity of 86.3 between MRC sponge and MRC coral rubble. The main species driving this dissimilarity were *P. anguicomus* (15.1 % contribution in the average dissimilarity), *Candidae* sp. (10.9 %), and *A. neglectus* (10 %), all of which were more abundant in MRC sponge. *Parazoanthus anguicomus* (14.6 %), *R. beaniana* (10.8 %) and *Candidae* sp. (8.7 %) were the species leading the average dissimilarity of 89.4 recorded between MRC sponge and LM

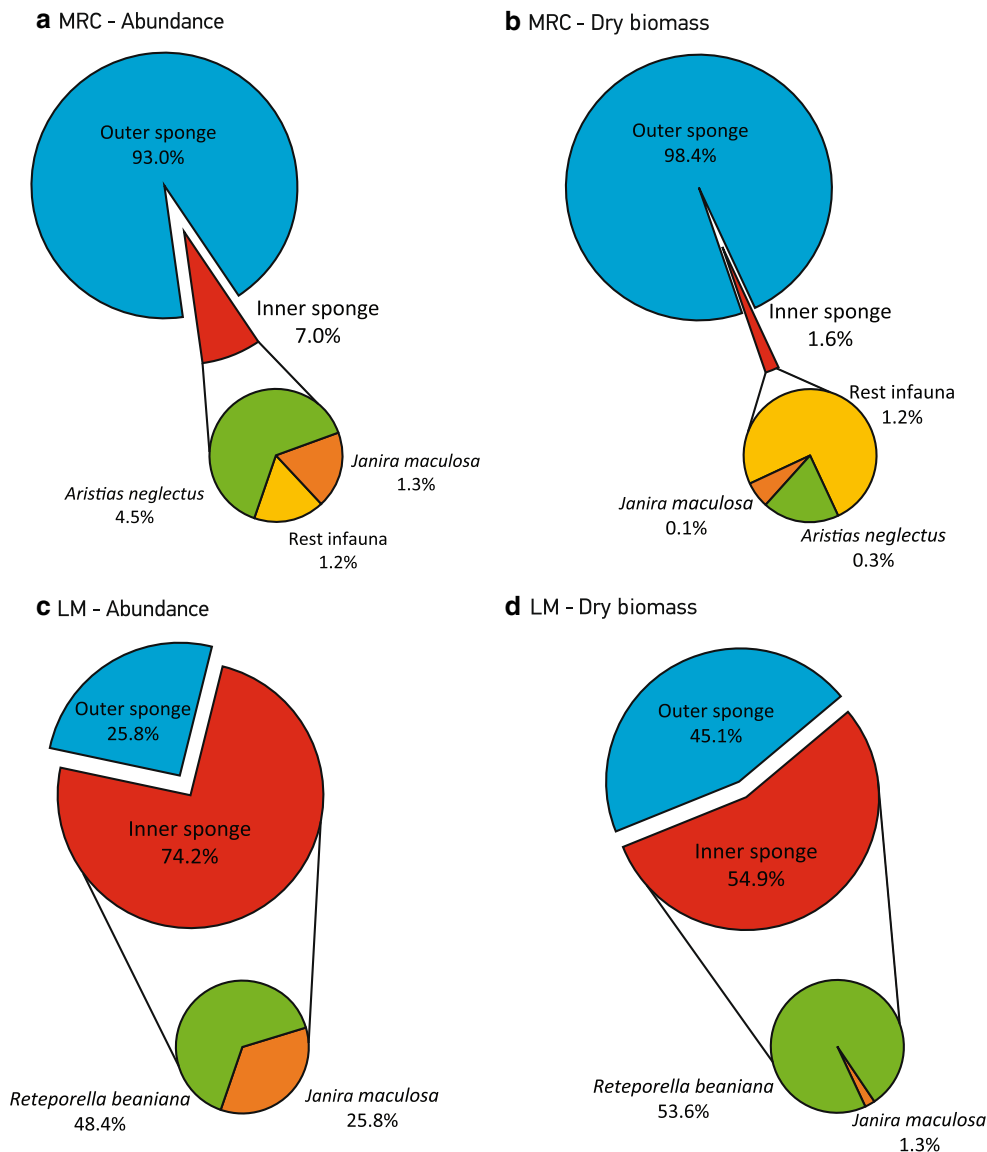


Fig. 4 Charts showing the shares of sponge sessile epifauna (“outer sponge”) and sponge infauna (“inner sponge”) in terms of abundance (total number of individuals) and dry biomass (total mg) in Mingulay Reef Complex (MRC) and Logachev Mound (LM)

sponge. The average dissimilarity between MRC coral rubble and LM coral rubble was 88.5; the species *A. nodulosa*, *Parazoanthus anguicomus*, and *Pseudamussium sulcatum* had a cumulative contribution of 48.4 %. The average dissimilarity between LM sponge and LM coral rubble was 89.3. This dissimilarity was mainly attributed to the species *A. nodulosa* (17.1 %), *R. beaniana* (15.3 %), and *J. maculosa* (11.6 %). SIMPER analysis based on dry biomass cm^{-3} microhabitat revealed overall similar patterns to those described above for abundance. Exceptions include a leading contribution of *Poecillastra compressa* to the average dissimilarity between MRC sponge and MRC coral rubble, and MRC sponge and LM sponge. In addition there was a leading contribution of

Pseudamussium sulcatum to the average dissimilarity between LM sponge and LM coral rubble.

Diversity indices, number of species cm^{-3} , number of individuals cm^{-3} , and dry biomass cm^{-3} microhabitat for sessile fauna and sponge infauna

There were no significant differences for the parameters H' and J' in most of the examined pairs of groups. Statistically significant differences were found for the number of species cm^{-3} , number of individuals cm^{-3} , and dry biomass cm^{-3} microhabitat (Table 4; Fig. 6a–f). The number of individuals cm^{-3} and dry biomass cm^{-3} microhabitat were lower in LM sponge than MRC sponge samples, while the

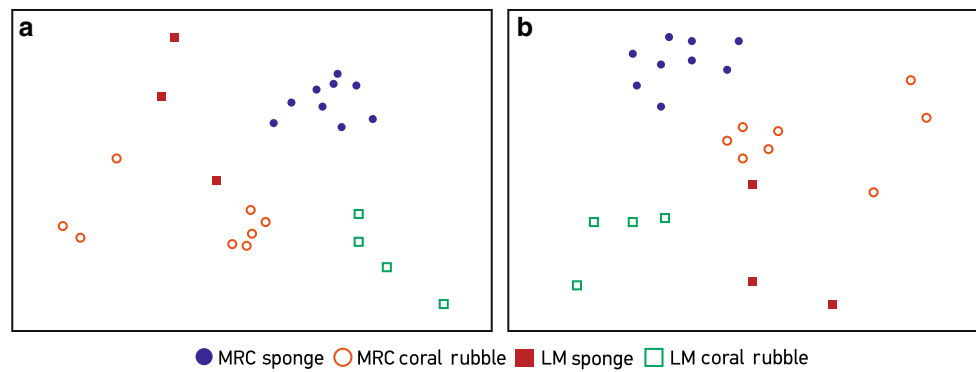


Fig. 5 2D nMDS plots of sponge and coral rubble microhabitats in Mingulay Reef Complex (MRC) and Logachev Mound (LM) based on number of individuals cm^{-3} microhabitat (a) and dry biomass cm^{-3}

microhabitat (b). Data were fourth-root transformed and were used in the calculation of Bray–Curtis similarities. Stress values were 0.14 and 0.11 in (a) and (b), respectively

Table 3 Results of analysis of similarities (ANOSIM) for number of individuals cm^{-3} and dry biomass cm^{-3} in the Mingulay Reef Complex (MRC) and Logachev Mound (LM) sponge and coral rubble microhabitats

Pairs of groups		Individuals cm^{-3}		Dry biomass cm^{-3}	
		<i>R</i>	<i>p</i> level	<i>R</i>	<i>p</i> level
MRC sponge	MRC coral rubble	0.681	0.001	0.624	0.001
MRC sponge	LM sponge	0.981	0.005	0.985	0.005
MRC coral rubble	LM coral rubble	0.467	0.014	0.517	0.01
LM sponge	LM coral rubble	0.944	0.029	0.981	0.029

R-statistic (*R*) and *p* level are given

opposite pattern was recorded between MRC coral rubble and LM coral rubble samples (Fig. 6a–f).

Correlation of microhabitat volume with *S*, *H'*, *J'*, total number of individuals, and total dry biomass for sessile fauna and sponge infauna

For MRC sponge samples, correlation analyses revealed a significant relationship between sponge volume and total species number *S* ($r = 0.74$, $p = 0.023$), sponge volume and total number of individuals ($r = 0.84$, $p = 0.004$), and sponge volume and total dry biomass ($r = 0.78$, $p = 0.011$). Significant correlations were also found for MRC coral rubble samples between coral volume and total number of individuals ($r = 0.72$, $p = 0.029$). In all other cases, there were no statistically significant correlations between the volume of the microhabitat and the examined parameters.

Distribution of feeding types for sessile fauna and sponge infauna

The fauna in the *S. coralliophaga*–coral rubble association included various feeding types (Fig. 7). At both locations, the sessile fauna that was living in the sponge or coral

rubble microhabitats was composed mainly of suspension/filter feeders (Fig. 7).

Discussion

Methodological considerations

Due to logistical constraints (i.e., ROV time, availability of space in the biobox), it was not possible to collect coral rubble not colonized by *S. coralliophaga* during our survey. As sponges affect the small-scale hydrography and food supply in their vicinity (e.g., Maldonado et al. 2012), abundance and biomass of epifauna near the sponge might be slightly higher compared to coral rubble not colonized by *S. coralliophaga*, and our data hence overestimate average abundance and biomass. Sponge size and morphology between MRC and LM, on the other hand, were similar and therefore unlikely to have affected the comparison between sites. Similarly, the levels of species richness, abundance, and biomass described in the present study should be regarded as underestimates since (1) only a small number of associations could be examined in each location (due to logistical constraints), (2) a number of small motile species living in association with the

Table 4 Results of analysis of variance for comparisons of Mingulay Reef Complex (MRC) and Logachev Mound (LM) sponge and coral rubble microhabitats for number of species $S\text{ cm}^{-3}$, Shannon–Wiener Index H' , Pielou’s evenness Index J' , number of individuals cm^{-3} and dry biomass cm^{-3}

	MRC sponge– MRC coral rubble	MRC sponge– LM sponge	MRC coral rubble– LM coral rubble	LM sponge–LM coral rubble
$S\text{ cm}^{-3}$	0 ^{#,***}	−1.2522 [†]	2.2688 ^{a,‡}	−1.0081 [†]
H'	0 ^{#,***}	7 [#]	27 [#]	0.3672 [†]
J'	0.4113 [‡]	4.6382 ^{†,***}	−1.1469 [†]	−4.4656 ^{‡,*}
Individuals cm^{-3}	0 ^{#,***}	1 ^{#,**}	2.0556 ^{a,‡}	9 [#]
Dry biomass cm^{-3}	−3.5807 ^{‡,***}	−3.3382 ^{‡,***}	2.9308 [‡]	2.0696 [†]

Values of two-sample t test[†], Welch’s two-sample t test[‡], Wilcoxon rank sum test[#] and p values (*** $p \leq 0.001$, ** $0.001 < p \leq 0.01$, * $0.01 < p \leq 0.05$, where no asterisks are shown, differences were not statistically significant) are given

^a Data were square-root transformed

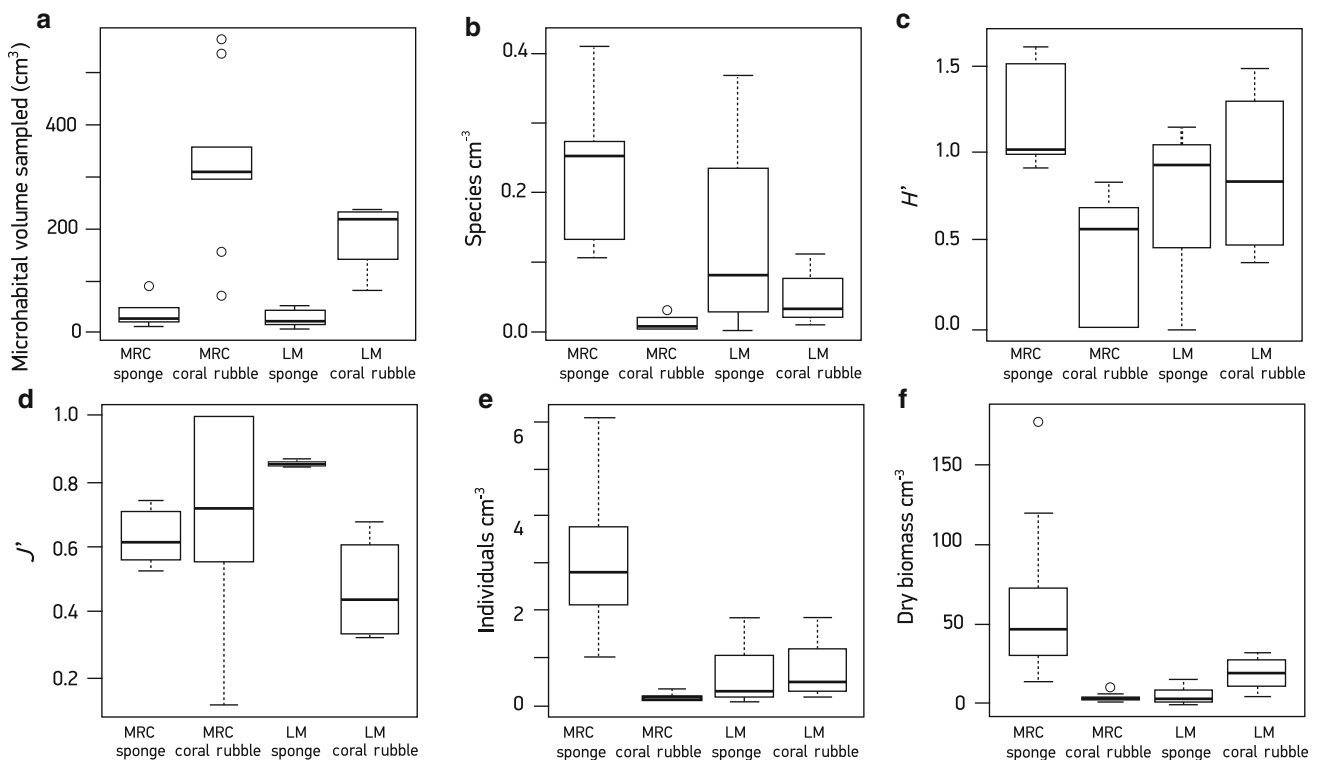


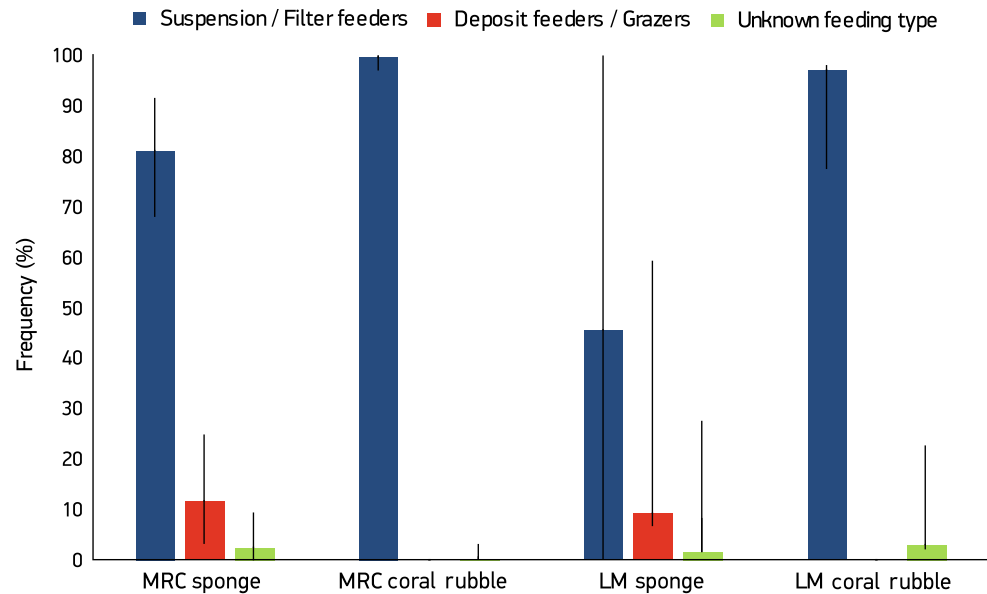
Fig. 6 Box plots of **a** microhabitat volume sampled (cm^3), **b** species number cm^{-3} microhabitat, **c** Shannon–Wiener Index, H' , **d** Pielou’s evenness Index, J' , **e** number of individuals cm^{-3} microhabitat, **f** dry

biomass cm^{-3} microhabitat in Mingulay Reef Complex (MRC) and Logachev Mound (LM). Lower and upper whiskers denote the data range (minimum–maximum values not considered to be outliers)

demosponge–coral rubble association could have escaped during the sampling procedure, and (3) a number of fragile specimens were too heavily damaged during sampling to be identified and thus were excluded from any abundance/biomass/diversity calculations. We therefore conclude that diversity at our study sites is comparable to a number of studies from shallow-water sites (e.g., Voultsiadou-Koukoura et al. 1987; Çinar et al. 2002; Neves and Omena 2003

and references therein; Ribeiro et al. 2003; Padua et al. 2013) where conditions enabled more comprehensive sampling. Finally, it should be mentioned that the risk of the cross-over by coral rubble fauna to the sponge during collection of samples from the seafloor was excluded since the comparisons between sponge and coral rubble microhabitats took into account solely the sessile fauna and sponge infauna.

Fig. 7 Relative contribution (%) of feeding types of sessile fauna and sponge infauna to each of the microhabitats in Mingulay Reef Complex (MRC) and Logachev Mound (LM). Calculations based on back-transformed data of arcsine numbers. Bars denote the mean values. Error bars show upper and lower 95 % CI



Differences in community structure and possible drivers

The nMDS and ANOSIM analyses on MRC and LM community structure showed distinct differences between the two regions. The small number of common species between the two regions, and the fact that species with high abundance/biomass in one region (i.e., the anthozoan *Parazoanthus anguicomus* in MRC, the bryozoan *Reteporella beaniana* in LM) occurred in low abundance/biomass in the other, indicate that patterns of species' bathymetric distributions were an important driver of differences in community structure between MRC and LM (Henry and Roberts 2007; Roberts et al. 2009; Henry et al. 2013b; van Soest and de Voogd 2013). Apart from species' bathymetric distributions, environmental parameters (e.g., speed of bottom currents, quantity and quality of food) may also play a role. Higher values of primary productivity at MRC than LM (Fehling et al. 2012) and higher concentrations of polyunsaturated fatty acids (PUFAs) on the MRC (Duineveld et al. 2012) versus the LM seafloor (Kiriakoulakis et al. 2007) are likely to have favored the development of a species-rich epifaunal community of suspension feeders recorded on the outer surfaces of MRC sponges. The development of this species-rich epifaunal community has likely further benefited from higher current speeds in MRC (up to 60 cm s⁻¹; Davies et al. 2009) than LM (up to 30 cm s⁻¹; Duineveld et al. 2007; Mohn et al. 2014).

Interestingly, diversity/abundance/biomass was higher in LM coral rubble than in MRC coral rubble, in contrast to findings between MRC sponge and LM sponge communities. The high values of abundance/biomass in LM coral

rubble are attributed to *Pseudamussium sulcatum* and especially to *Asperarca nodulosa* whose bathymetric distribution extends from the sublittoral zone to the abyss (Oliver and Allen 1980). Bivalves are often reported as inhabitants of sponge canals (e.g., Çinar et al. 2002; Ribeiro et al. 2003; Schejter et al. 2012; Padua et al. 2013), but the relatively large size of *A. nodulosa* prevents it from settling in the canals of *S. coralliophaga* and thus specimens live attached to underlying coral rubble (see also Voultsiadou-Koukoura et al. 1987; Gherardi et al. 2001; Neves and Omena 2003). In contrast to the LM coral rubble, abundance and biomass of suspension/filter feeders in the MRC coral rubble was low; enhanced water flow conditions, and thus oxygenation/food supply, support the presence of suspension feeders in the LM coral rubble (Lenihan 1999; McQuaid and Mostert 2010; Whitman and Reidenbach 2012). This is particularly interesting, given that bottom currents are stronger at MRC than LM (see above) and supports the suggestion that small-scale gradients of environmental conditions can favor the proliferation of specific feeding types/taxonomic groups, which in turn can have an impact on community species composition, abundance and biomass (Çinar et al. 2002 and references therein).

The importance of small-scale gradients in the configuration of community structure is further highlighted by the comparison between MRC sponge and MRC coral rubble; high water movement on sponge surface facilitates the presence of a species-rich community of suspension feeders (Peattie and Hoare 1981; see also Raes and Vanreusel 2006). In both MRC sponge and coral rubble, the anthozoan *Parazoanthus anguicomus* was among the species with high values of abundance and biomass, which had an

important contribution to the higher similarity that was found when comparing MRC sponges to MRC coral rubble than LM sponges to LM coral rubble. This species' high abundance and biomass are likely due to its high fecundity (Ryland 2000) and flexibility in feeding (Buhl-Mortensen 2001; Mueller et al. 2014).

The role of *S. coralliophaga* as a biological structure

Previous studies on sponge associates have revealed species-rich communities inhabiting sponge canals (e.g., Westinga and Hoetjes 1981; Duarte and Nalesso 1996) and sponges acting as a nursery ground (Schejter et al. 2012; Padua et al. 2013) providing shelter against strong currents (Peattie and Hoare 1981) and/or predators (Magnino et al. 1999a). In contrast to previous studies on sponge infauna, we recorded only a small number of species living inside *S. coralliophaga* at both MRC and LM. The reasons for this are unclear but the facts that only a few small specimens were found inside the sponges and that a number of bivalves and brachiopods were found to be overgrown by *S. coralliophaga*, suggest that the conditions inside *S. coralliophaga* probably do not favor infaunal organisms (Magnino et al. 1999b; Skilleter et al. 2005). The most abundant infaunal species was the amphipod *Aristias neglectus* which has low host specificity and has been found across various invertebrates (Vader 1983; Kilgallen 2010); its presence in the vascular cavities of sea anemones has been related to feeding on partially digested food particles (Vader 1983) and thus its presence inside *S. coralliophaga* may also be related to its feeding on food particles captured by the sponge.

The sessile fauna colonizing *S. coralliophaga* and coral rubble at MRC and LM was mainly composed of cnidarians, molluscs, and bryozoans. Previous studies on the faunal composition of coral rubble zones in the North Atlantic Ocean have revealed that their sessile fauna is rich in cnidarians (Roberts et al. 2008; Wienberg et al. 2008) and sponges (Freiwald and Wilson 1998; Freiwald et al. 2002; Purser et al. 2013). In addition, cnidarians and molluscs had the highest number among sessile species in Porcupine Seabight samples from on- and off-mound sites (Henry and Roberts 2007), while bryozoans were the most speciose group among sessile fauna inhabiting blocks of live and dead corals in the Faroe Shelf (Jensen and Frederiksen 1992). Finally, bryozoans and hydroids had the highest number of sessile species in reef framework habitats in the MRC (Henry et al. 2013a).

The colonization of the outer surface of *S. coralliophaga* by a diverse community of sessile suspension feeders in MRC suggests that this sponge acts as a major settlement substrate in that region (see also Klitgaard 1995; Montenegro-Gonzalez and Acosta 2010; De Campos et al.

2012; Padua et al. 2013). This is further emphasized by the much higher species richness, abundance, and dry biomass in MRC sponges compared to MRC coral rubble. In addition, each of these two microhabitats had a different combination of characteristics (e.g., hydrography, food supply) that increased habitat complexity and underpinned species coexistence and thus enhanced benthic biodiversity (McGuinness and Underwood 1986; Stuart et al. 2003; Hewitt et al. 2008; Schaal et al. 2011; Buhl-Mortensen et al. 2010; Padua et al. 2013). In contrast to MRC, *S. coralliophaga* did not act as a biological structure in LM; this fact is probably due to a combination of factors including species' bathymetric distributions, bottom currents, and food supply in LM (see above for details).

The taxonomic composition of the *S. coralliophaga*–coral rubble associations in MRC closely resembles the fauna described in Henry et al. (2013a) for that region; this high similarity indicates that the organisms living in association with *S. coralliophaga* and underlying coral rubble constitute a subset of the benthic fauna of the wider MRC area. On this basis we suggest that the relationship between *S. coralliophaga* and its inhabitants is largely facultative (see also Klitgaard 1995). The close resemblance between *S. coralliophaga*–coral rubble association and wider MRC fauna suggests that (1) the collection of *S. coralliophaga*–coral rubble associations could be used as an alternative, less-destructive approach (e.g., compared to box-coring) for future studies on reef biodiversity (2) *S. coralliophaga*–coral rubble associations could be used for studies of structure and functionality of CWR food webs. Finally, our findings highlight the necessity for studies in the ecology of deep-sea sponge grounds (Hogg et al. 2010; Bo et al. 2012; Beazley et al. 2013).

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